



Breathing is coupled with voluntary initiation of mental imagery

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ABSTRACT

Previous research has suggested that bodily signals from internal organs are associated with diverse cortical and subcortical processes involved in sensory-motor functions, beyond homeostatic reflexes. For instance, a recent study demonstrated that the preparation and execution of voluntary actions, as well as its underlying neural activity, are coupled with the breathing cycle. In the current study, we investigated whether such breathing-action coupling is limited to voluntary motor action or whether it is also present for mental actions not involving any overt bodily movement. To answer this question, we recorded electroencephalography (EEG), electromyography (EMG), and respiratory signals while participants were conducting a voluntary action paradigm including self-initiated motor execution (ME), motor imagery (MI), and visual imagery (VI) tasks. We observed that the voluntary initiation of ME, MI, and VI are similarly coupled with the respiration phase. In addition, EEG analysis revealed the existence of readiness potential (RP) waveforms in all three tasks (i.e., ME, MI, VI), as well as a coupling between the RP amplitude and the respiratory phase. Our findings show that the voluntary initiation of both imagined and overt action is coupled with respiration, and further suggest that the breathing system is involved in preparatory processes of voluntary action by contributing to the temporal decision of when to initiate the action plan, regardless of whether this culminates in overt movements.

1. Introduction

Recent research on brain-body interactions has shown that bodily signals from internal organs have influence on a broad neural network of cortico-subcortical regions (Herrero et al., 2018; Ito et al., 2014; Klimesch, 2018; Kluger and Gross, 2021), and play an important role in diverse sensory-motor functions (Allen and Friston, 2018; Azzalini et al., 2019; Critchley and Harrison, 2013; Garfinkel and Critchley, 2016; Park and Blanke, 2019), beyond homeostatic reflexes. One line of research has investigated how the respiratory system is associated with non-olfactory cognitive functions including memory retrieval (Heck et al., 2019; Zelano et al., 2016), fear discrimination (Zelano et al., 2016), visuospatial processing (Perl et al., 2019), and it has been further proposed that respiration entrains cortical oscillatory activities (e.g., theta and gamma oscillations) (Kluger and Gross, 2021; Lakatos et al., 2019; Tort et al., 2018). On the other hand, another line of research has

demonstrated that breathing is involved in motor processes such as running in mammals (Bramble and Carrier, 1983) and orofacial movements in mice (Kurnikova et al., 2017; Moore et al., 2013). While these previous studies revealed that breathing is associated with low-level motor outputs, which are mostly repetitive and rhythmic (Moore et al., 2014), a recent study further reported that the breathing system is also linked with the initiation of voluntary action control, the ability to initiate an action based on one's own will (Park et al., 2020). More specifically, this study reported that the phase of respiration is coupled with the onset of a voluntary hand movement, and with its neural precursor, the so-called readiness potential (RP), suggesting that the breathing system is involved in a high-level motor cognition. In the current study, we asked the question of whether breathing-action coupling is limited to voluntary "motor actions" that are associated with overt movements (with muscle contraction) or whether the breathing system also influences "mental actions" which do not involve any overt movement.

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We thus tested whether breathing is associated with the voluntary initiation of two types of mental imagery, namely motor imagery (MI) and visual imagery (VI). MI involves the mental simulation of actual motor execution, based on the generation of a complete motor preparation program without any overt motor output (Jeannerod and Decety, 1995). Previous work has demonstrated that such MI performance is associated with cortical activation within the premotor (e.g., supplementary motor area; SMA) and motor cortices (e.g., precentral gyrus) (Héту et al., 2013), as well as changes in autonomic nervous activity (e.g., heart rate, respiratory rate) comparable to those seen during actual motor execution (Decety et al., 1993). VI refers to the internal generation of the visual experience of a particular scene without the presence of the corresponding sensory input from the environment (Dijkstra et al., 2019; Kosslyn et al., 2001; Pearson et al., 2015). VI has been conjectured to be a weak form of visual perception, with which it shares many of the same neural mechanisms (Dijkstra et al., 2019; Pearson et al., 2015). To test our hypothesis, participants performed a modified Libet paradigm (Libet et al., 1983), a classical behavioral paradigm for measuring the onset of self-initiated actions, with three different types of motor and mental tasks: motor execution (ME), MI, and VI.

Regarding the underlying mechanisms of breathing-action coupling, a recent study proposed that interactions between the breathing system and voluntary actions occur to minimize potential competition between motor commands originating during the production of voluntary hand motion and those arising from the involuntary breathing motor system (Park et al., 2020). Voluntary action has been suggested to be composed of three stages: (1) formation of intention (2) preparation of action, and (3) action execution (Haggard, 2008). In our experimental design, the three experimental conditions (i.e., ME, MI, VI) would share comparable first two stages of voluntary action (i.e., intention and preparation of action), whereas the required type of action execution is different. Thus, our current study was designed to investigate at which stage (i.e., intention-preparation or execution) such breathing-action coupling occurs. On the one hand, if such competition requires overt movement and occurs during the action execution stage, breathing-action coupling would be observed only during ME, but not in either of the mental imagery tasks. On the other hand, if breathing-action coupling occurs at the intention-preparation stage, such an interaction would also be observed in the mental imagery conditions (i.e., MI, VI). We further separated the MI and VI conditions to test whether different types of mental imagery (motor vs. visual) have a differential influence on breathing-action coupling. For instance, if breathing-action coupling requires the involvement of motor cortical activity, it would be observed in MI but not VI, as MI still activates the motor cortex (Héту et al., 2013). On the other hand, if breathing-action coupling occurs in the cortical areas associated with more general action planning, such as SMA (Nachev et al., 2008), it would be observed in both MI and VI conditions. In addition, our experimental design with a simultaneous recording of EEG signals during these tasks provides the opportunity to test whether the generation of the RP requires overt movement or whether the RP is associated with intention and preparation of action, a question that has largely been overlooked in the literature (Alexander et al., 2016). We here report that (1) the respiratory phase was coupled with the voluntary initiation of mental imagery performance, (2) the RP waveforms were observed while the participants were performing mental imagery tasks, and (3) the RP amplitude was coupled with the respiratory phase.

2. Methods

2.1. Participants

Thirty-five participants (17 female; 1 left-handed; mean age: 25.9 ± 4.1 years) took part in the study and reported no history of cardiovascular disease or neurological or psychiatric disorders. All participants signed a written informed consent form and were paid for their

participation. All procedures were approved by the local ethics committee (Commission Cantonale d'Ethique de Genève). One participant was excluded from analysis due to excessive movement-related artifacts in the EEG data, which contaminated > 50% of trials. Also, one participant was excluded because of the impaired trigger signals due to a technical problem during the recording. The data from thirty-three subjects were analyzed.

2.2. Paradigm

During the motor execution (ME) task, participants performed the classical Libet task (Libet et al., 1983), as described below. Throughout the task, participants put their right index finger on the keypad and were instructed to press the button at any time they wanted to. A trial started when a red dot appeared at a random location of the clock face (radius: 2° of visual angle) and participants were instructed to fixate a dot at the center of the clock face. The red dot always rotated only one full cycle for 10.24 s. Participants were instructed to wait for at least a quarter rotation (i.e., 2.56 s), and press the button before the end of one full rotation. Following previous studies, we asked the participants to refrain from (1) pre-planning the interval between the start of the trial and the button press, and (2) using regular intervals between the start of the trial and the button press (Libet et al., 1983; Schurger et al., 2012). The red dot then further rotated another quarter cycle and disappeared. After 0.5 s, the dot reappeared at a random location, and participants were instructed to report the timing of the button press by moving the location of the clock hand using the keypad.

During the motor imagery (MI) task, participants were instructed to imagine pressing the key whenever they wanted to, but without actually moving their fingers. Except for the instruction regarding their performance, every procedure was identical to the ME condition. At the end of each trial, participants reported the estimated timing of when they performed the MI task. During the visual imagery task (VI), we wanted the participant to perform a mental action that does not involve any motor component (i.e., neither motor execution nor motor imagery) while maintaining the level of visual input and attention similar to the other two tasks (i.e., ME, MI). Thus, we developed a simple non-motoric VI task, still utilizing the rotating clock hand. Participants were instructed to imagine stopping the clock hand rotation whenever they wanted to. Then at the end of each trial, the participants retrospectively reported the estimated timing of when they conducted the VI task. Participants conducted three blocks (i.e., a total of 75 trials) of each task. Of note, participants always performed the VI task before the other two tasks. This was to prevent participants from thinking about motor processes (e.g., motor inhibition) during the VI task. For instance, a previous study showed inhibition of a motor response could generate RP-like waveforms (Misirlisoy and Haggard, 2014), which could confound our experimental design. In other words, when participants were performing the VI task, they did not know that there are other conditions potentially using motor imagery or execution. Participants then conducted the remaining six blocks of ME and MI, in a randomized order.

2.3. Physiological data recordings

Continuous electroencephalography (EEG), electrocardiography (ECG), electromyography (EMG), and respiratory signals were collected using an EEG amplifier (EEGO system; ANT Neuro) at a sampling rate of 1024 Hz. EEG signals were recorded with a 64-channel cap (Waveguard cap; ANT Neuro). Bipolar ECG electrodes were placed over the right shoulder and the left side of the abdomen. Bipolar EMG electrodes were placed over the flexor digitorum superficialis muscle. Respiratory signals were recorded using a respiration belt (Piezoelectric respiration belt; SleepSense) placed over the chest.

2.4. Analysis of the RP

All preprocessing was conducted using the Fieldtrip toolbox (Oostenveld et al., 2011). EEG data were offline filtered between 0.1 and 40 Hz, following a recent suggestion that a high pass filtering at 0.1 Hz effectively removes infra slow oscillations when computing slow cortical potentials (Garipelli et al., 2011). Independent component analysis was conducted and stereotypical independent components reflecting eye movements and eye blinks were excluded (Delorme and Makeig, 2004). EEG data were re-referenced to a common average reference, following recent RP studies (Park et al., 2020; Schultze-Kraft et al., 2016). The RP was then computed from EEG signals locked to the button-pressed time (ME condition) or retrospectively reported time (ME, MI, VI conditions), within the 5 sec time window (-4 to 1 s regarding the respective markers). Trials showing excessive noise (> 3 SD) were excluded from further analysis. Because RPs are typically observed in fronto-central regions (Park et al., 2020; Schultze-Kraft et al., 2016), we report RP results averaged over six electrodes (i.e., Cz, C1, C2, FCz, FC1, FC2) placed over the fronto-central region (see Fig. 3b). For testing the existence of a significant RP waveform, we compared the RP amplitude of individual samples in the active time window (-2 to 0 s regarding the action onset) to the mean of EEG amplitude in the baseline time window (-4 to -3 s), using a dependent sample t-test across all participants. Multiple comparisons in the temporal dimension were corrected using a cluster-based permutation test (Maris and Oostenveld, 2007). The permutation p -value corresponds to the proportion of shuffled maximal cluster-level statistics (500 times) that exceeds the observed original cluster-level test statistics.

2.5. Analysis of the EMG signal

Time-frequency representations (i.e., power) of EMG signals were calculated using a wavelet transform (Tallon-Baudry et al., 1996) for the frequency range from 10 to 40 Hz (in 0.2 Hz step), within the 2 s time window (-1 to 1 s regarding the markers for the performance onset in each task; in 50 ms step). Single trial EMG data were convolved by a complex Morelet's wavelet: $w(t, f_0) = A \cdot \exp(-t^2/2\sigma_t^2) \cdot \exp(2i\pi f_0 t)$, using a constant ratio of $f_0/\sigma_f = 5$ where $\sigma_f = 1/2\pi\sigma_t$, and the normalization factor $A = (\sigma_t \sqrt{\pi})^{-1/2}$ (Tallon-Baudry et al., 1996). Movement-induced EMG signals were tested for through a dependent sample t-test across all participants (active time window: -1 to 1 s; baseline time window: -1 to -0.8 s) in each frequency band separately, and FDR corrected p -values were computed (Benjamini and Hochberg, 1995).

2.6. Analysis of breathing-action coupling

Coupling between the respiratory phase and the action (i.e., ME, MI, VI) onset was tested using a permutation based two-step procedure, mainly because the distribution of the breathing phase is not uniform. First, the respiratory phase was computed by applying the Hilbert transform to the bandpass filtered respiration signal between 0.2 and 0.8 Hz. We then concatenated the respiratory phase values at the timing of action events from all the participants, separately in each condition. Then, as a first-level statistics, we applied the non-parametric Hodges-Ajne test (Ajne, 1968), which assesses the uniformity of the circular data without making specific assumptions about the underlying distribution, using the Circular Statistics Toolbox (Berens, 2009). The Hodges-Ajne test computes a test statistic (i.e., M) defined as the minimum number of data points that can be observed in half of the circle, and the null hypothesis of uniform distribution is rejected when the test statistic is smaller than the expected numbers (Ajne, 1968). Of note, the duration of expiration is known to be longer than the duration of inspiration, indicating that even random events that are independent of the respiratory phase will be more likely observed during expiration than the inspiration phase. To resolve this bias, we compared the original statistics with the null

distribution of surrogate statistics that are obtained from surrogate respiration data whose phase values are randomly shifted. This permutation procedure corrects such bias because the only difference between original and surrogate statistics is the temporal relationship between the action onset and breathing signal. For that, the single-trial respiratory data was cut into two segments with a random amount, and the order was swapped. We created 500 surrogate statistics that define the chance-level coupling between the respiration phase and the action onset. A permutation p -value was then computed as the proportion of the statistics obtained from shuffled data that exceeded the original statistic.

2.7. Analysis of breathing-RP coupling

To test the coupling between the respiratory phase and the RP amplitude, we first computed the mean RP amplitude as a function of the respiratory phase (i.e., 6 equally sized bins with the step size of 60°) in each trial (within -4 ~ 0 s time window regarding the action onset). Then, obtained mean RP amplitudes were normalized in each trial by subtracting the mean RP amplitudes across 6 respiratory phase bins from the individual RP amplitude in each bin (see Fig. 4a). The degree of coupling between the RP amplitude and the respiratory phase across single trials was then quantified per subject by computing a non-parametric circular-linear correlation coefficient across all trials (Mardia, 1976). Correlation coefficients across participants were then summed as a test statistics for the following permutation test. The statistical significance of the summed correlation coefficient was tested through a permutation test using surrogate respiration data at the group level, as described above.

3. Results

3.1. Respiratory phase is coupled with voluntary initiation of motor execution

Because the mental action tasks (i.e., MI and VI; see below) do not involve any motor execution (i.e., keypress), we estimated the onset of mental actions based on participants' retrospective reports (Alexander et al., 2016). Thus, before analyzing the MI and VI data, we first checked whether participants' retrospective reports were able to provide reliable temporal markers in our experimental set-up, by analyzing the data obtained in the ME condition. During the ME task, participants performed the modified Libet paradigm (Libet et al., 1983), and were instructed to press the key whenever they wanted while looking at a clock face with a rotating red dot. At the end of each trial, participants retrospectively reported their estimate of the time at which they pressed the key. The waiting time for the ME performance based on the retrospective report (6.17 ± 0.68 sec; mean \pm SD) was significantly shorter compared to the waiting time based on the button-pressed time (6.30 ± 0.66 sec; $t_{32} = 2.28$, $p = 0.029$), which is in accordance with the previously reported bias effect (Libet et al., 1983). Next, we computed breathing-action coupling separately for each of these two markers (i.e., button-pressed time and retrospectively reported time). As revealed by a two-step procedure combining the Hodges-Ajne and permutation tests (see Methods), breathing was significantly coupled with the voluntary hand movement onset both when using the button-pressed time (Fig. 1a, b; permutation test, $p = 0.002$) and when using the retrospectively reported time (Fig. 1d, e; permutation test, $p = 0.006$). The grand mean respiration phase at the moment of ME performance was observed during the late expiration phase using both markers (i.e., between $\pi/2 \sim \pi$; see the red dots in Fig. 1a, d).

Throughout the experiment, we also measured electromyography (EMG) activity to confirm whether the required task performance was accompanied by finger movements (i.e., muscle contraction), in particular during the MI and VI tasks. During the ME task, we observed significant EMG activity regardless of the temporal markers used, with the EMG signal amplitude being weaker in the report-based analysis compared to

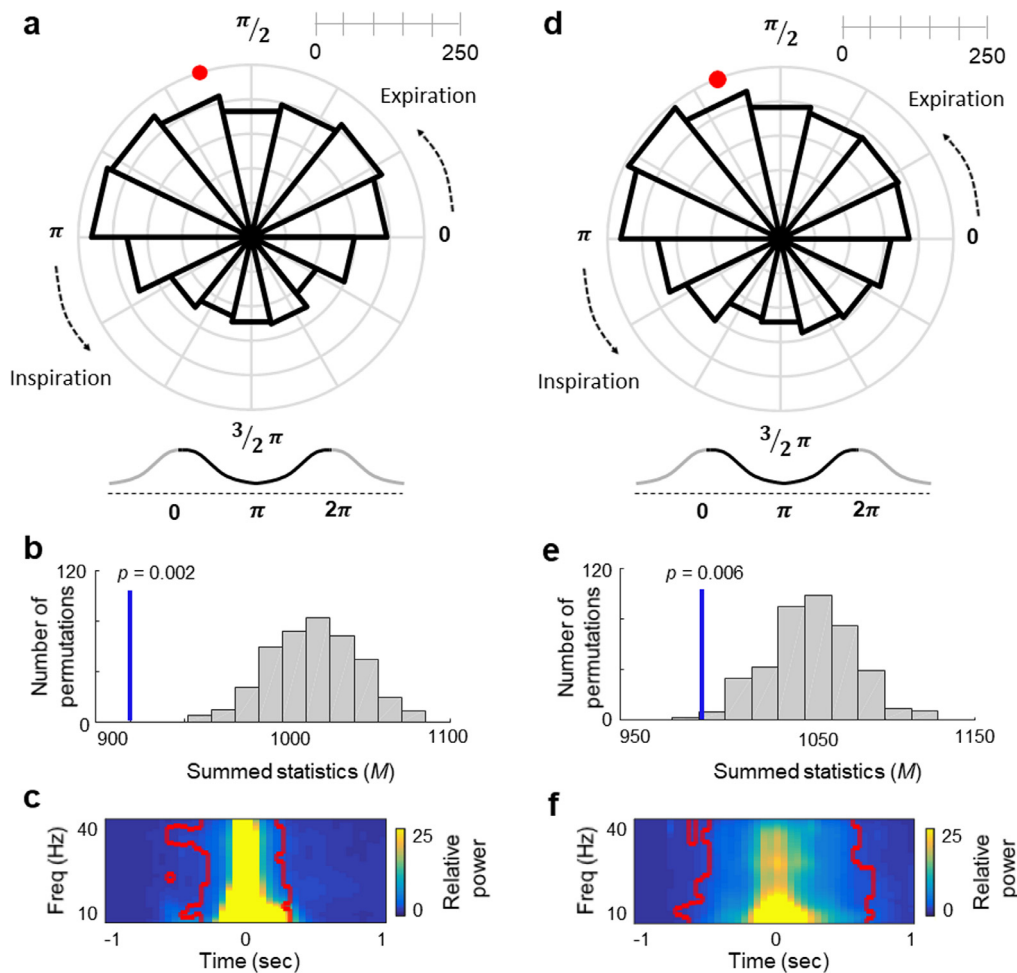


Fig. 1. Coupling between voluntary initiation of motor execution (ME) and respiratory phase. **a** Distribution of respiratory phases at the timing of voluntary ME ($N = 33$), analyzed by using the button-pressed time. Participants voluntarily initiated ME more frequently during the late phase of expiration. The red dot indicates the grand-averaged respiration phase (i.e., a circular mean across all participants) at the timing of the button press. The scale bar on the top-right indicates the number of action onsets in the polar histogram. **b** Histogram of the statistics (M , Hodges–Ajne test, see Methods) obtained from surrogate respiratory phase data in the ME condition. The blue vertical line indicates the statistic obtained from the original respiratory phase data. The statistic from original data was significantly smaller than chance-level statistics obtained from phase-shifted surrogate respiration data (permutation $p = 0.002$). **c** Time-frequency analysis of EMG data confirmed that ME was accompanied by muscle activity. The samples within the red contour lines indicate significant ones (FDR corrected $p < 0.01$). **d** Distribution of respiratory phases at the timing of voluntary ME ($N = 33$), analyzed using the retrospectively reported time. **e** Histogram of the statistics obtained from surrogate respiratory phase data in the ME condition, analyzed using the retrospectively reported time. The blue vertical line indicates the statistic obtained from original respiratory phase data (permutation $p = 0.006$). **f** Time-frequency analysis of EMG data confirmed that ME based on participants' retrospective reports was accompanied by muscle activity (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

the keypress-based analysis (Fig. 1c, f; dependent sample t-test between baseline [-1 to -0.8 s] and active time window [-1 to 1 s]; The samples within the red contour lines indicate significant ones at FDR corrected $p < 0.01$). These results in the ME condition (1) replicate our previous report that the onset of voluntary hand movement is synchronized with the expiratory breathing phase (Park et al., 2020) and (2) confirm that the retrospective report on the timing of action performance can provide a reliable temporal marker when overt behavioral markers are not available, such as during the MI and VI conditions in our experimental set-up (Alexander et al., 2016).

3.2. Respiratory phase is coupled with the voluntary initiation of motor imagery

Next, we tested whether the breathing cycle is coupled with the voluntary initiation of MI performance. During the MI task, participants performed a modified Libet paradigm in which they were instructed to

imagine pressing the key whenever they wanted to, but without actually pressing it (see Methods). At the end of each trial, participants retrospectively reported the timing of when they imagined pressing the key. Participants waited for 6.09 ± 0.74 sec on average until they conducted the MI task. We found a significant coupling between the onset of MI performance and the respiratory phase of late expiration (Fig. 2a, b; permutation test, $p = 0.008$). EMG analysis revealed the absence of significant muscle activity when participants performed the MI task (Fig. 2c; all FDR corrected $p > 0.05$).

3.3. Respiratory phase is coupled with voluntary initiation of visual imagery

We next tested whether the breathing phase is associated with the timing of voluntary initiation of VI performance. For that, participants carried out the modified Libet paradigm and were instructed to imagine stopping the rotation of the clock hand whenever they wanted (see

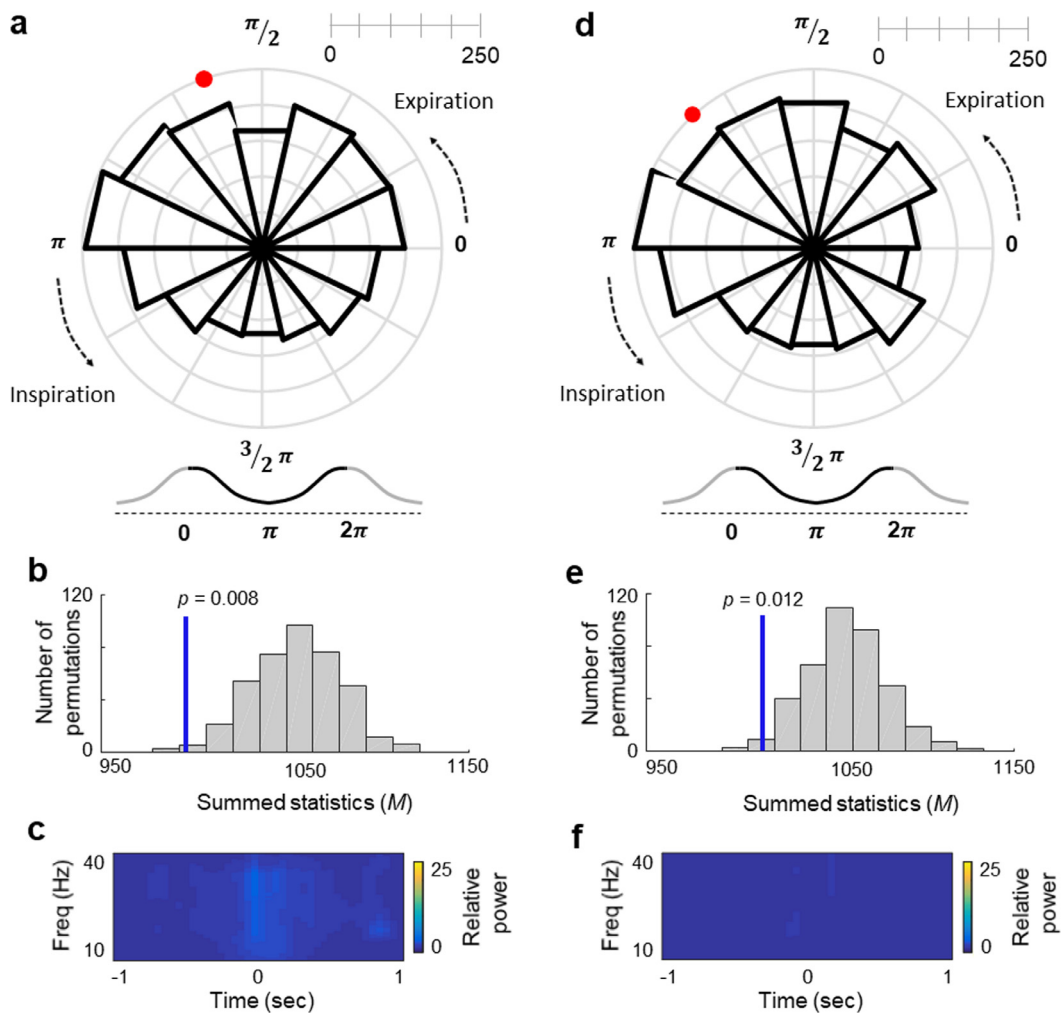


Fig. 2. Coupling between voluntary initiation of mental imagery (e.g., motor and visual imagery; MI, VI) and respiratory phase. **a** Distribution of respiratory phases at the timing of MI performance ($N = 33$). Participants voluntarily initiated MI more frequently during the late phase of expiration. The red dot indicates the grand-averaged respiration phase (i.e., a circular mean across all participants) at the timing of MI. The scale bar on the top-right indicates the number of action onsets in the polar histogram. **b** Histogram of the statistics (M , Hodges–Ajne test, see Methods) obtained from surrogate respiratory phase data in the MI condition. The blue vertical line indicates the statistic obtained from the original respiratory phase data. The statistic from the original data was significantly smaller than the chance-level statistics obtained from the phase-shifted surrogate respiration data (permutation $p = 0.008$). **c** Time-frequency analysis of EMG data confirmed that the MI performance was not accompanied by finger muscle movements. **d** Distribution of respiratory phases at the timing of voluntary VI performance ($N = 33$). **e** Histogram of the statistics obtained from surrogate respiratory phase data in the VI condition. The blue vertical line indicates the statistics obtained from original respiratory phase data (permutation $p = 0.012$). **f** Time-frequency analysis of EMG data confirmed that the VI performance was not accompanied by finger muscle movements (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Methods). At the end of each trial, participants retrospectively reported the timing of when they performed this VI task. According to the reports, participants waited for 6.18 ± 0.71 sec on average. We found a significant coupling between the timing of VI performance and the late expiratory breathing phase (Fig. 2d, e; permutation test, $p = 0.012$). Again, no EMG activation was observed during the VI task (Fig. 2f; all FDR corrected $p > 0.05$).

After participants completed all experiments, we asked them whether they had been aware of any relationship between their breathing or heartbeat and the required performance (Q1), and whether they had used their breathing or heartbeat to perform the required task (Q2), separately for each condition. In accordance with our previous report (Park et al., 2020), most participants responded ‘No’ to both (Q1) and (Q2) for all three tasks (number of ‘Yes’ responses to [Q1, Q2] among 33 participants for ME: [2, 1]; MI: [1, 2]; VI: [3, 1]), suggesting that participants were unaware of the relationship between breathing cycle and the respective task performance.

3.4. Slow negative EEG drift precedes the onset of motor imagery and visual imagery

Before analyzing the RP during MI and VI conditions, we first checked whether the RP could be observed using the retrospective reports in the ME condition. Significant RP waveforms were indeed seen when using both the retrospectively reported time and button-pressed time (Fig. 3a, dependent sample t-test between baseline [-4 to -3 s] and active time window [-2 to 0 s]; black and yellow double lines indicate samples with permutation $p < 0.05$ in the ME condition when using button-pressed time and retrospective report, respectively). The RP amplitude computed using reported time was weaker (i.e., less negative) compared to the RP amplitude computed based on the key-pressed time. This result confirms that retrospectively reported time provides a reliable marker for RP analysis when a more objective behavioral marker (i.e., key-pressed time) cannot be collected during MI and VI tasks (Alexander et al., 2016).

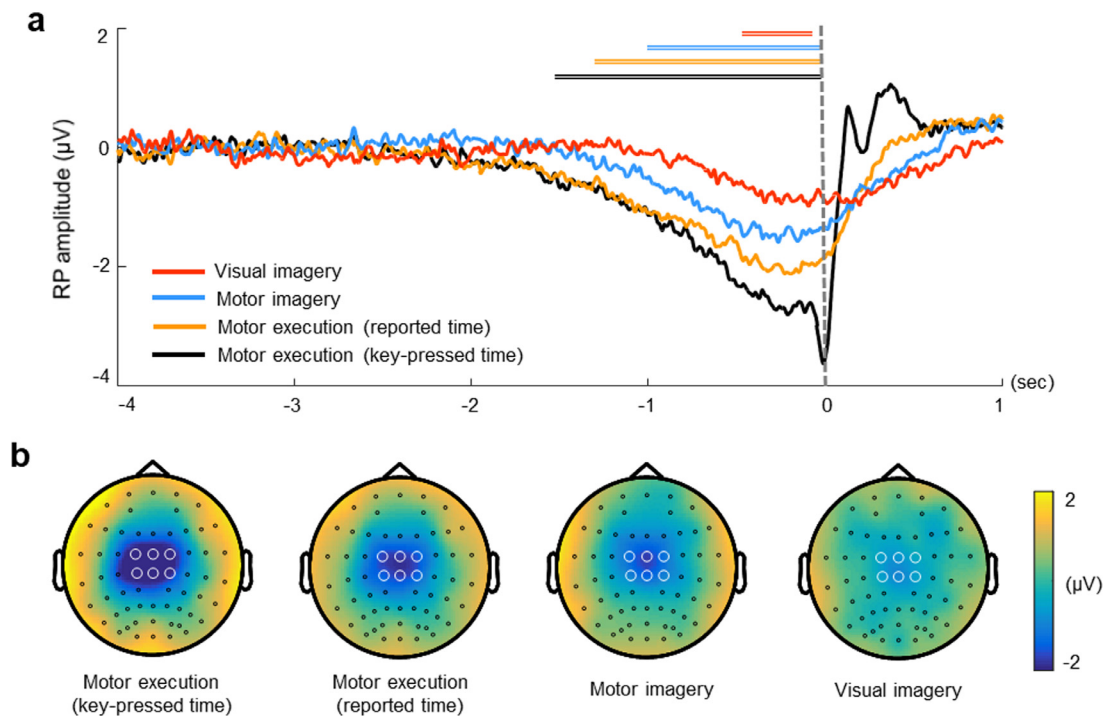


Fig. 3. The readiness potential (RP) during motor execution (ME), motor imagery (MI), and visual imagery (VI) tasks. **a** RP waveforms obtained from six fronto-central electrodes for ME with key-pressed time (black), ME with retrospectively reported time (orange), MI (blue), and VI (red). [-4 to -3 s] time window was set as a baseline period. The colored double lines above indicate the time window that significant RP was observed in the correspondingly colored RP waveforms (permutation $p < 0.05$). **b** RP topographies in differential experimental conditions in [-0.5 to 0 s] time window. White circles indicate the electrodes used for computing the RP waveforms shown in a (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Next, we tested whether the RP waveforms could be observed in the MI and VI conditions. Although RP amplitude was smaller during MI and VI conditions, with respect to the ME-related RPs, we observed significant RP waveforms in both conditions (Fig. 3a, dependent sample t-test between baseline [-4 to -3 s] and active time window [-2 to 0 s]; blue and red double lines indicates samples with permutation $p < 0.05$ in MI and VI conditions, respectively). The presence of RPs in the MI and VI conditions suggest that the RP is not specifically linked to the preparation of an overt movement (see Discussion).

3.5. Coupling between the RP amplitude and the respiratory phase

We then tested whether the RP amplitude correlates with the phase of respiration, to replicate a recently reported finding (Park et al., 2020). Given that (1) we observed similar breathing-action coupling in all three conditions (i.e., ME, MI, VI), that (2) the RP waveforms were observed in all three conditions, and that (3) it has been suggested that analyzing single-trial RP data is extremely difficult, therefore necessitating a denoising process (Schurger et al., 2021), we merged data from the three conditions to increase the signal to noise ratio for analyzing the coupling between the RP amplitude and respiratory phase. As shown in Fig. 4, we found that the respiratory phase correlated with the amplitude of the RP (permutation test, $p = 0.002$; see Supplementary Fig. 1 for the results in each condition). This result shows that the RP amplitude is more negative during the expiration phase compared to the inspiration phase, replicating our previous finding (Park et al., 2020).

3.6. Modulation of interbeat intervals around action onset

Finally, we checked the evolution of interbeat intervals around the action onset as breathing and heartbeat are interrelated. More specifically, it is well known that heartbeats decelerate during expiration and accelerate during inspiration, a phenomenon so-called respiratory sinus

arrhythmia (Hayano et al., 1996). Thus we expected that such modulation of heartbeats would be observed around the onset of actions which was synchronized with the expiration phase. For that, we analyzed five consecutive interbeat intervals (i.e., interval between 2 ECG R-peaks) surrounding action onset. We pooled interbeat interval data across three conditions (i.e., ME, MI, VI), as we did not expect potential difference of interbeat intervals across conditions (see Supplementary Fig. 2 for results in each condition). As shown in Fig. 5, interbeat interval gradually increased before (i.e., A-1, A-2) participants initiated voluntary action and decreased after (i.e., A+1, A+2) they conducted the action (repeated measure ANOVA across five interbeat intervals; $F_{4,128} = 16.81$, $p < 0.0005$). Because we found that participants breathed out before the voluntary action and breathed in after the action performance, this result shows that the phenomenon of respiratory sinus arrhythmia also occurs around the action onset in the present conditions.

4. Discussion

Our main finding is that respiration is coupled with the voluntary initiation of mental actions which do not involve any overt movement. In previous work, we reported an association between the breathing cycle and voluntary hand movements (Park et al., 2020). Although voluntary hand movement could be considered as a higher-level motor function, compared to the repetitive, involuntary, rhythmic motor movements (e.g., whisking in rodents and running in mammals) that have been linked to breathing previously (Bramble and Carrier, 1983; Moore et al., 2013), the question whether breathing cycle is associated with voluntary initiation of mental actions not involving overt motor movement has remained unexplored. The current study demonstrates that the breathing system is involved in the preparatory processing of voluntary mental actions, beyond overt hand movements. Our EEG analysis further showed that the RP, which has been suggested to be associated with the preparation of self-initiated movements (Schurger et al., 2021), precedes the

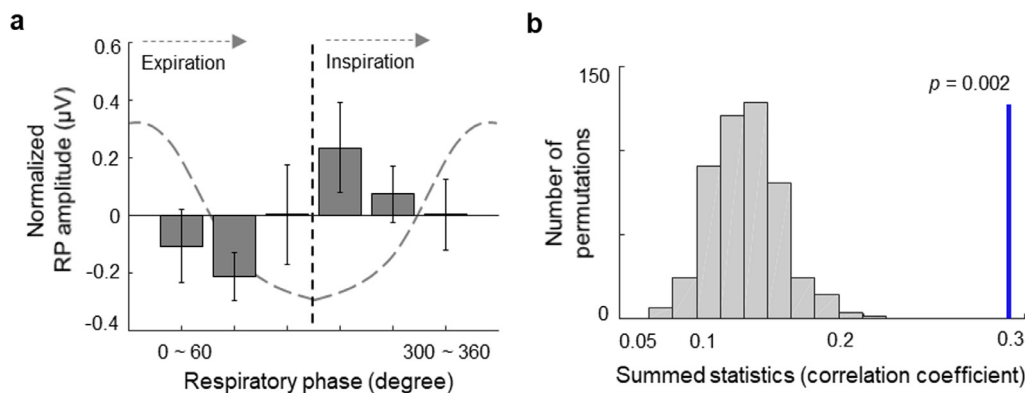


Fig. 4. Coupling between the RP amplitude and respiratory phase. **a** The RP amplitude as a function of six bins of the respiratory phase (from 0 to 360°). Error bars represent the s.e.m. The RP amplitude was more negative during the expiration compared to the inspiration period. **b** Histogram of the statistics (i.e., non-parametric circular-linear correlation coefficients) obtained from surrogate respiration data whose phase was randomly shifted. The blue vertical line indicates the statistic from the original respiration data. The result of the permutation test confirms that the correlation coefficient from original respiration data is significantly larger than chance-level correlation coefficients obtained from surrogate respiration data (permutation $p = 0.002$), confirming the presence of coupling between the RP amplitude and respiratory phase (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

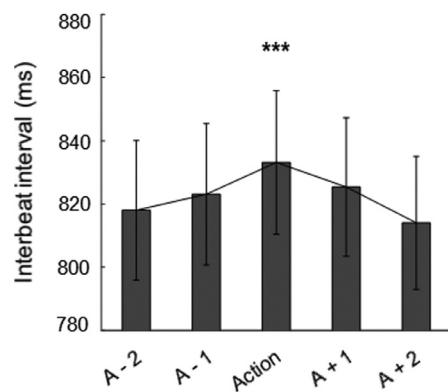


Fig. 5. Modulation of five interbeat intervals around the voluntary action onset. Interbeat interval was largest when participants were performing the voluntary action (Action; interval between two consecutive ECG R-peaks surrounding the onset of action). Interbeat interval increased before the action onset (A-2, A-1) whereas it decreased after the action onset (A+1, A+2; repeated measure ANOVA across five interbeat intervals, $p < 0.0005$). Error bars represent the s.e.m. *** $p < 0.0005$.

voluntary initiation of mental actions (both MI and VI), suggesting that the RP does not require subsequent motor movement, and is further coupled with the respiratory phase.

4.1. Breathing-action coupling in mental imagery

We observed that the participants unconsciously preferred to imagine pressing the button (i.e., MI) while breathing out (i.e., expiration) even though they had complete freedom regarding when to perform the task. Previous research reported that continuous MI performance (e.g., imagining of locomotion or exercise for several minutes) induces changes in physiological states including heart and respiration rate, changes that are proportional to the amount of mental effort needed (Decety et al., 1993, 1991). The authors further suggested that MI recruits, at least partly, the same physiological mechanisms as genuine motor actions. Our experimental design differed from these previous reports in that participants were instructed to imagine a single discrete movement (i.e., a single keystroke) in a self-initiated manner, thereby mentally simulating the single, discrete finger movement present in the classical Libet paradigm. We further observed that participants were

more likely to perform the VI task, namely to imagine stopping the clock hand rotation, during the expiration phase compared to the inspiration phase although they were not aware of this. Inspired by a previous study (Alexander et al., 2016), we designed the VI task requiring participants to visually imagine stopping the rotating dot on the screen in a self-initiated manner. This was developed in order to include an experimental condition that does not involve any motor processes (i.e., an actual motor process as in the ME condition nor an explicit imagined motor process as in the MI condition), while still requiring participants to perform a mental action task with the same experimental set-up for the Libet paradigm. In addition, participants performed the VI task before the ME or MI tasks, to prevent them from using a motor inhibition strategy, a type of motor processing that is known to induce the RP (see below) (Misirlisoy and Haggard, 2014). During these mental imagery tasks, as predicted, our EMG data confirmed that MI and VI performance was not accompanied by the muscle activity typical of overt finger movements.

Our behavioral results during the MI and VI conditions provide evidence that helps to identify the mechanisms of breathing-action coupling. In our previous study (Park et al., 2020), we proposed that voluntary action is more likely to occur during the passive phase of the breathing cycle (i.e., expiration phase) in order to avoid competition between two co-occurring motor processes originating from the involuntary-respiratory motor and voluntary-hand motor systems. If this is the case, how could the breathing system still be involved in the processes of voluntary actions without overt motor output? Voluntary actions have been proposed to comprise three distinctive stages (Haggard, 2019, 2008). First, the intention of the action is formulated, believed to recruit the prefrontal cortex and basal ganglia. Second, the intended action is prepared, mainly deciding when the action will be performed, recruiting the supplementary motor complex (SMC), which is composed of the SMA, supplementary eye field, and pre-SMA (Nachev et al., 2008). The RP has been argued to arise during this phase (Haggard, 2008). Finally, motor signals, via MI, are relayed to the corresponding muscle groups through the corticospinal tract, leading to action execution. What we observed is that the MI task is already sufficient to evoke breathing-action coupling. This finding strongly suggests that breathing-action interactions do not necessitate overt motor movements (discrete hand-finger movements in the present case), and instead occur at the stages of intention and action preparation, that come prior to the motor execution. Interestingly, we further observed that participants still preferred to perform the VI task while breathing out, similarly to during ME and MI tasks. Taken together, these results further suggest that the breathing system is involved in a more general preparatory process that contributes to

temporal decisions regarding when to execute an action program even when it is not involved in actual (i.e., ME) or imagined (i.e., MI) motor processes.

4.2. The RP precedes mental actions

We observed that a slow drift of neural activity preceded the onset of the MI and VI performance. Different types of brain potentials have been observed while subjects were waiting for different types of motor actions or stimuli: these potentials include the RP (Kornhuber and Deecke, 2016), contingent negative variations (CNV) (Walter et al., 1964), and stimulus-preceding negativity (SPN) (Brunia, 1988). These brain potentials have very similar spatio-temporal distributions and are usually categorized according to the behavioral paradigm applied (Schurger et al., 2021). It has been argued that the RP occurs when actions are self-initiated and irregular (rather than involuntary and regular) (Jankelowitz and Colebatch, 2002). On the other hand, the CNV is observed during a fixed interval between a warning cue and an involuntary motor response to an imperative stimulus (Walter et al., 1964), whereas the SPN does not require a motor response (either voluntary or involuntary), and is observed while participants were anticipating task-relevant stimuli such as feedback on their performance (Brunia, 1988). Based on these past findings and the present data in our behavioral paradigm, requiring self-initiated actions without external cues, we suggest that the present brain potential observed during MI and VI reflects the RP, rather than CNV or SPN.

Surprisingly few studies have investigated whether overt movement and muscle contractions are necessary for generating the RP. In other words, mental actions without any motor processing are sufficient to generate the RP? Although a few studies have investigated whether voluntary initiation of MI can generate the RP-like waveforms, they were characterized by several limitations that prevent strong conclusions from being drawn (Cunnington et al., 1997; Jankelowitz and Colebatch, 2002; Niazi et al., 2013). For instance, participants in some such studies were instructed to imagine the movement in response to an external cue whose interval was regular, making it more similar to CNV than to the RP (Cunnington et al., 1997; Jankelowitz and Colebatch, 2002). Another study asked participants to imagine a movement in a self-initiated manner with irregular intervals but they were also instructed to perform an actual motor execution around two seconds after the imagined performance in order to mark the onset of MI, thereby making it difficult to distinguish between neural activity preceding imagination and actual muscle movement (Niazi et al., 2013). A more recent study directly tested whether a mental decision without a motor response can evoke the RP (Alexander et al., 2016). In this study, participants were instructed to conduct either a mental decision task (i.e., choosing one letter among four letters) or the same mental decision followed by a button press. Although the results suggested that mental decisions without motor processing can generate the RP, the study had several limitations. First, the decision task involved rapid serial visual stimulation (RSVP), which could confound the RP result due to the visual-evoked potential component. Our VI protocol avoided such non-essential additional visual stimuli, with the amount of visual input fully comparable across tasks. Second, in the earlier study, the order of the two conditions was randomized. Thus, participants might presumably have tried to inhibit their motor response during the decision-only condition to properly perform the task, and this would be problematic as it has been shown that inhibitory motor processes can generate RP-like waveforms (Misirlisoy and Haggard, 2014). In order to minimize such inhibitory responses in the VI condition, our participants always performed the VI task before ME and MI conditions. Taken together, we propose that our results provide new clear evidence suggesting that (1) the RP does not necessarily require muscle movement or motor execution, and (2) the RP accordingly reflects a more general preparatory process in voluntary action programs.

4.2.1. Breathing-RP coupling and its underlying neural mechanism

Finally, we observed that the amplitude of the RP was coupled with the phase of respiration (i.e., more negative RP amplitude during the expiration compared to the inspiration period), replicating our recent finding (Park et al., 2020). What neural mechanisms might underlie such interactions among breathing, voluntary action planning, and the RP? Previous animal research has suggested that the SMC is the main neural source of the RP (Nachev et al., 2008). The SMA, however, is also activated when just observing a graspable object without movement, suggesting its involvement in motor planning processes (Grèzes and Decety, 2002), which may explain why we were able to observe the RP during a MI task that does not require overt movement. Furthermore, the SMC has been associated with cognitive action control such as initiation, inhibition, or switching to a new action plan or sequence (Nachev et al., 2008), suggesting its functional role is not limited to motor action programs. Accordingly, we observed the RP even when participants were planning VI performance devoid of overt movement and of explicit movement imagery. Interestingly, a different line of research suggests that the SMA is also involved in the control of breathing. Whereas previous research has shown that the SMA is mainly involved in conscious control of volitional breathing (Colebatch et al., 1991) or constrained breathing (Raux et al., 2007), a more recent TMS study further demonstrated that the SMA is also involved in the control of spontaneous breathing at rest (Laviolette et al., 2013). Thus, together with our findings, currently available evidence suggests that such interactions among spontaneous breathing, general action preparation, and the RP involve premotor and motor systems in the SMC. A follow-up study should identify the actual neural sources underlying our observation, potentially using high-density EEG or MEG combined with structural MRI.

To conclude, we here demonstrate that voluntary initiation of mental actions (both MI and VI), which did not involve any overt movement by our participants, is intimately coupled with the breathing system. Such imagined mental actions are also sufficient to generate the RP, the amplitude of which was further coupled with the breathing cycle. Uncovering the close interrelationship between breathing control, planning for motor and mental actions, and the RP, we propose that the breathing system contributes to voluntary action preparation, specifically regarding when to perform an internally generated action plan, irrespective of any subsequent motor process. Lastly, we further suggest that our findings provide empirical evidence which could support and extend recent neuroscientific theories of consciousness proposing that specific bodily signals and their neural representation contribute to neural mechanisms of consciousness (Azzalini et al., 2019; Blanke and Metzinger, 2009; Damasio and Carvalho, 2013; Northoff and Lamme, 2020; Northoff and Zilio, 2022; Park and Blanke, 2019; Tumati et al., 2021). Whereas most of these previous embodied consciousness models have focused on brain-heart interactions and their role in perceptual aspects of consciousness, either sensory awareness (Park et al., 2014; Salomon et al., 2016) or self-consciousness (Aspell et al., 2013; Park et al., 2016), our findings further suggest that the breathing system is another important source of bodily signals contributing to consciousness and self-consciousness, in particular to the action-related aspect of conscious experiences such as voluntary action and potentially the sense of agency (Haggard, 2017; Serino et al., 2022).

Declaration of Competing Interest

H.D.P., O.A.K. and O.B. are inventors on a provisional patent application PCT/IB2020/050858 (Title: Method and system for determining the intention of performing a voluntary action) held by the Swiss Federal Institute (EPFL). O.B. is cofounder and shareholder of Metaphysics Engineering SA. O.B. is member of the board and shareholder of Mind-maze SA.

Credit authorship contribution statement

Hyeong-Dong Park: Conceptualization, Formal analysis, Data curation, Writing – review & editing. **Timothy Piton:** Conceptualization, Formal analysis, Data curation. **Oliver A. Kannape:** Conceptualization, Writing – review & editing. **Niall W. Duncan:** Conceptualization, Writing – review & editing. **Kang-Yun Lee:** Writing – review & editing. **Timothy J. Lane:** Writing – review & editing. **Olaf Blanke:** Conceptualization, Writing – review & editing.

Data Availability

The datasets generated from this research are not publicly available because the human participants from whom the data were collected have not consented to their public release. However, deidentified are available on request from the corresponding author.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.neuroimage.2022.119685](https://doi.org/10.1016/j.neuroimage.2022.119685).

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